

The geobiological interface: Granitic outcrops as a selective force in mammalian evolution

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Abstract

Granite outcrops appear with regularity in various parts of the world. They may be associated with mountains, or they may appear in areas that today have little other topographic relief than the outcrops themselves. Wherever granitic agglomerations are found, however, their influence on the biota of a region is profound. Rocks influence both microhabitat and macrohabitat for plants and animals. In some cases, the rocky habitats permit a more mesic microhabitat to develop within a generally more xeric region. Such microclimatic influences may permit the establishment of trees and the maintenance of green leaves, even during droughts. For mammals, in addition to the increased availability and predictability of food, the rock habitat itself provides shelter, amelioration of climatic variables and, in some cases, a resource that is defensible by the mammals. However, the rock habitat is one that also demands special adaptations by mammals that specialize toward a rupicolous existence. Such specializations include morphological, ecological, and behavioral traits that develop in direct response to the selective forces required to inhabit rocks. These influences may extend even to mating systems, where the unusual habit of harem polygyny develops among small mammals whose males manage to defend the rock resource against other males, thereby accruing females. Because of their influence on macro- and microhabitat, granite outcrops also have a regional influence on biodiversity, increasing significantly the number of species that occur in areas that are frequently rather depauperate due to their semiarid or arid nature. The responses of mammal faunas in Africa and South America to granite outcrops is used to compare and assess the importance of these rock outcrops on aspects of mammalian biology.

Introduction

The diversity of mammals in any particular region has been related to many factors, including climate, age of the fauna, past formation of refugia, productivity, environmental predictability, competitors and predators, size of the area, and other factors (see Rosenzweig 1995 for review). In general, the effect of physical structure of the environment (as opposed to the biotic structure) on patterns of diversity and richness has been given less attention, although there has been some work on the effects of dunes on small mammal species richness (Brown 1973). Even in this study, however, the dunes have been considered mainly as habitats that supported fewer species of mammals than the surrounding better-vegetated areas. In a more detailed analysis of regional patterns of species diversity, Brown (1975), found that in a xeric North American desert system, overall species diversity of rodents is strongly influenced not only by α -diversity (species occurring in a single locality), but by β -diversity (species turnover) as well, since many species have restricted distributions in deserts. Of course, at a macroscale, the influence of mountain ranges and other major topographic features has long been known to have a major influence on species richness through increased habitat diversity, altitudinal effects, refugial formation, and other factors (e.g. Simpson 1964; Wilson 1974; Brown 1978; Mares & Ojeda 1982; Mares 1992; Willig & Sandlin

1991). At a smaller scale, the influence of structural features of the environment on patterns of mammalian diversity and richness are less apparent.

One regularly occurring structural feature of habitats scattered throughout the world is granite outcrops. As has been shown in other papers in this issue, the influence of these outcrops on plants, microorganisms, animals, and people are extensive. There has not been a great deal of research on the influence of granite outcrops on mammals, although there are some notable exceptions, particularly in examining the influence of rocks on the biology of small mammals in southern Africa and South America. Hoeck (1975, 1982) and Hoeck *et al.* (1982), for example, studied hyraxes in the Serengeti and found that the rocks themselves were a critical resource. The males of these rock specialists defended the rock-piles in such a way that they were able to attract and keep multiple females as mates. The females also required access to the rocks for food, water, protection, and nesting space. Thus the male hyraxes, by virtue of being able to control access to the rocks, formed harems; harem polygyny is an unusual behavioral trait in a small mammal. Lacher (1981) studied a caviid rodent *Kerodon rupestris* (guinea pig family) in eastern Brazil, that was also highly specialized for living on granitic outcrops within a larger dry tropical scrubland, the Caatinga. He found that *Kerodon*, which strongly resembled a hyrax externally, also defended rock-piles and, like the hyraxes of Africa, also accrued females to form harems.

In a multivariate comparison of morphological, ecological, and behavioral characteristics of rock-dwelling

small mammals from throughout the world, Mares & Lacher (1987) showed that mammals inhabiting rocks have developed a host of similar adaptations, including specific morphological, ecological, and behavioral traits, such as specialized foot structure, general body form, dietary similarities, similar activity periods, alarm calls, communal defaecation, and a propensity to form harems. The formation of harems seems to result from the ability of the males to defend portions of the rock-piles, thus controlling a resource that is required by the females and their offspring. In order for a female to have access to the critical rock resource, and all of the ecological factors associated with the rocks, she must enter into the harem of the male. Mares & Lacher interpreted this to be an example of resource defense polygyny (Emlen & Oring 1977), a pattern that has also been documented for such non-rock specialists as tree-dwelling bats (the Neotropical emballonurid, *Saccopteryx bilineata*) that control access to cavities in the trees by defending them against other males, thus developing harems of females that require access to the hollow tree in order to raise their young (Bradbury & Emmons 1974). Mares & Lacher (1987) also made clear that becoming a rock specialist requires a broad array of adaptations. Moreover, these adaptations are similar from one part of the world to another, regardless of the phylogenetic history of the organisms in question (they examined 24 species of mammals in 17 genera, 12 families and 4 orders).

At a larger scale, rocks have also been shown to have an influence on the regional species richness of small mammals, especially in southern Africa, where this phenomenon has been examined in some detail. Coetzee (1969), for example, noted that "The distribution of animal life (especially the small mammals) is largely

influenced by rocky outcrops"; he provided a list of 28 species of mammals that frequent rocky outcrops in Namibia. He later (Coetzee 1983) supported these observations with an analysis of mammalian geographic ranges. In a more detailed ecological study in Namibia, Withers (1979) examined the small mammals of an inselberg (isolated rocky outcrop) community and found that both rock specialists and more-generalist species comprise the community. The community ecology of the mammals was greatly affected by microclimate effects of the inselberg and its associated vegetation, as opposed to the surrounding sparse desert habitat. Although he did not conduct a regional analysis of distributional patterns, Withers showed clearly that the rock-piles were a major factor in small mammal species richness in the Namib Desert. Among the areas used by Mares & Lacher (1987) in their broadly comparative study of rock-dwelling mammals were the Namib Desert, the Caatinga, and the Andean region of Argentina. Mares *et al.* (1981) and Mares *et al.* (1985a) had shown that rock-piles in the Caatinga had a significant influence on both species richness and persistence, and Mares (1993) provided information showing that rocky habitats were important components of generic richness for small mammals in Andean deserts.

Here, I extend the comparisons of the Namib Desert, Brazilian Caatinga, and Argentine Andes to consider the effect of granite outcrops on the structure of the entire mammalian community in these three areas. I first provide a brief comparative review of the regions and their history to permit a greater understanding of how mammals have adapted to rock-piles, a significant abiotic structural component of their habitat in three markedly different drylands on two southern continents.



Figure 1. The interface of sand, river, and rock in the Namibian Desert near Gobabeb. The light-colored material in the foreground is sand at the edge of the riverine vegetation of the Kuiseb River. On the other side of the river are granitic outcrops. Barely visible in the background beyond the rocks is the gravel plain of the Namib. Both the rocky areas and the river support vegetation that is quite different from either of the two major habitats (the dune fields and the plains). The mammals of the rocks are also distinct from those of the other major habitats.



Figure 2. A broad granite surface exposure (lajeiro) in the Caatinga of northeastern Brazil. In the background are rocky outcrops (serras). Lajeiros collect water and form micro-communities of plants (evidenced by the cacti, shrubs and grasses in the center of the photo). Serras support shrub and tree communities that are distinct in physiognomy and persistence of green vegetation from the surrounding Caatinga scrub forest. The mammals of the lajeiros, serras, serrotes (larger outcrops that form small hills), and chapadas (outcrops that are larger still, forming small mountains) are very distinct from those of the non-rocky areas.

Methods

Study Areas

Namibia. The Namib Desert, a coastal desert, is one of the oldest deserts on earth (Seely 1987; Ward & Corbett 1990). It is also among the world's driest deserts, with much of the precipitation being received as fog (Walter 1986). Over much of the area there is only sparse vegetation, whether on the gravel plains or on the enormous dune "sea" that characterize the region. There are, however, areas that support much more vegetation than the habitats that surround them, and these include rivers (e.g. Kuiseb) and granite outcrops (inselbergs and other outcrops), where trees, shrubs, and grass may be present (e.g. Theron *et al.* 1980; Seely 1987). In some places, such as near the Desert Research Station at Gobabeb, the various habitats abut one another. Here fields of moving dunes pour over granitic outcrops that line the Kuiseb River valley, north of which an abrupt transition to gravel plains occurs (Fig 1). The history of the Namib region, as well as the general ecology of the desert and its flora, fauna, and habitats has been fairly well studied in recent years (e.g. Coetzee 1969, 1983; Stuart 1975; Joubert & Mostert 1975; Werger 1978; Henschel *et al.* 1979; Withers 1979; Tilson 1980; Tilson *et al.* 1980; Walter 1986; Seely 1987, 1990). Although seldom examined specifically, researchers have found that inselbergs play a major role in the maintenance of mammal species richness in this desert by virtue of the microhabitat provided by the rocks, which includes floristic and climatological influences.

Caatinga. The Caatinga of northeastern Brazil has also received a great deal of attention from biologists in recent years (e.g. Markham 1972; Eiten 1974; Webb 1974; Reis 1976; Ab'Sáber 1977; Lacher, 1981; Willig, 1983; Mares *et*

al. 1981, 1985a; Andrade-Lima 1982). This region of more than 650 000 km² lies well within the tropics and undergoes periodic pronounced droughts at irregular intervals during which most of the vegetation loses its leaves. Its vegetation is much like a thorn scrub in aspect. Populations of small mammals die back during the droughts, and there is great misery among the human inhabitants of the regions as livestock die and water for human use becomes scarce. During wet years, which are more common than dry years, the area is a lush, low, green forest and mammals and other wildlife species are abundant. During droughts, the Caatinga resembles the semiarid chacoan thorn scrub of western Argentina, including the presence of many types of tree cacti (*Cereus*) and other cacti that frequent the areas of open granite (termed "lajeiros" in Portuguese). The Caatinga also has granite outcrops varying in size from isolated boulder piles to small hills (Fig 2). It is in these outcrops that the area's only endemic mammal is found, the caviid rodent, *Kerodon rupestris*, a rupicolous species specialized for life on the isolated rock-piles. Mares *et al.* (1985a) hypothesized that these rock-piles play a major role in maintaining mammal diversity in the Caatinga by offering a microhabitat refuge to mammals during the periodic droughts. They suggested that after severe droughts, the Caatinga, especially the core of the region, is in large part re-colonized by small mammal populations that managed to persist in the more mesic microclimate associated with the rock-piles.

Argentine Andes. The Andes of westcentral Argentina also support vast areas of granite outcrops, interspersed with other types of rock (Videla & Suarez 1991), and with flat plains located between mountain massifs (Fig 3). The rocky areas of the Andes are also home to a number of rock specialists among small mammals (Mares



Figure 3. Rock outcrops in an inter-Andean valley near the town of Uspallata, Mendoza Province, Argentina at an elevation of about 2,000 m elevation. The scrub desert of the gravel plains, which mainly supports creosote bush (*Larrea*), gives way to different communities of plants on the rock outcrops. The area supports a number of mammals that are specialized for life in the rocks.

& Lacher 1987; Ojeda & Mares 1989; Mares 1993; Braun & Mares 1996). Much of the high Andes of Argentina includes arid habitats that support either sparse grasses or scattered shrubs (Mares *et al.* 1985b). Although the mammals of this region have not been as well studied as those of the previous two areas, the rocky areas appear to function as important microhabitats for species persistence through their effect on microclimate, plant distribution, and as places for shelter (*e.g.* Pearson 1948; Pearson & Ralph 1978).

Data

Published data on mammals and their habitats were examined for the three areas described above. In particular, information was sought that specifically referenced the use of rocks by the mammals in these regions. Species lists were examined for the areas in question, and information was obtained on surveys of the mammals of the areas that included information on the entire mammal fauna, rather than being limited to small mammals. References utilized are included throughout this report. Additionally, my students and I conducted extensive research on mammals of the Caatinga in the 1970s and on mammals in the Andean and pre-Andean mountains during the last three decades (*e.g.* Mares *et al.* 1989, 1997; Barquez *et al.* 1991). Additionally, I was able to spend a brief field period in Namibia in 1995.

Effects of Rock-piles

Few studies have considered the ecological effects of rock-piles on mammals. While not designed to measure the ecological effect of rocks on mammals *per se*, Withers (1979) found that the microclimate of the rocky inselbergs he examined supported different plant species from the surrounding desert, and this microhabitat-plant

association was related to the abundance of small mammals, as well as to small mammal species richness. Lacher (1981) and Streilein (1982a,b,c) also found that the rocky habitats provided refugia for small mammals during periods of drought, when the green vegetation and occasional pools of water offered escape from the harsh aridity of the surrounding habitat. Water availability has been shown to be an important factor in reproduction of small mammals in both Namibia and the Caatinga (Christian 1976, 1980; Withers 1979; Streilein 1982c,d), although no research has shown how water might effect small mammals in the Andes. Below, I discuss various effects of rocky habitats that are related to mammal occurrence. A taxonomic listing of mammals in these three areas, as well as indications as to whether or not the taxa are rock specialists, is given in Table 1, whereas a list of rock specialists in the three areas is given in Table 2.

Microhabitat effects of rocks

As noted, many studies have shown that rocky areas provide a microhabitat that differs significantly from the surrounding region. Clearly, the microhabitat effects of rocks on climate, plants, and animals are interrelated in complex ways, but it is instructive to tease apart the various factors that interact to influence mammals in order to understand more clearly the role that rocks play in patterns of mammalian richness and persistence. In the three arid to occasionally semi-arid habitats considered in this report, the rocky substrate contributes in the following ways to mammalian persistence and richness.

Structure. Rocks form a major structural component of the ecosystem, especially in areas that would have little topographic relief were it not for the rocks themselves. The structural effect of rocks can be considered to be a first-level effect of the rocks on the community of

Table 1

Orders, families, and genera of mammals inhabiting granitic outcrops in Namibia (in the general environs of Gobabeb); in the Brazilian Caatinga (near Exu, Pernambuco); and in the Andes of central Argentina (Mendoza Province). Rock specialists (species that are highly adapted to inhabit rocks and that are generally limited to rocky outcrops) are denoted by an asterisk (*). O = order; F = family. Common names are in parentheses. Based on information for Africa in Coetzee (1969), Stuart (1975), Withers (1979), Skinner & Smithers (1990); for Brazil in Mares *et al.* (1981, 1985), Streilein (1982a,b,c); for Argentina in Barquez *et al.* (1991), Mares (1993), Mares *et al.* (1985b, 1997), and Mares (unpublished data).

Namibia	Caatinga	Argentine Andes
O. Macrosceloidea	O. Didelphimorphia	O. Didelphimorphia
F. Macroscelididae (elephant shrews) <i>Elephantulus rupestris</i> * <i>Elephantulus intufi</i> <i>Macroscelides proboscideus</i>	F. Didelphidae <i>Monodelphis domestica</i> (Gray short-tailed opossum) <i>Didelphis albiventris</i> (White-eared opossum)	F. Didelphidae <i>Thylamys pusilla</i> (Mouse opossum)
O. Chiroptera	O. Chiroptera	O. Rodentia
F. Vespertilionidae <i>Eptesicus hottentotus</i> (Long-tailed house bat)	F. Molossidae <i>Molossops mattogrossensis</i> * (Flat-headed free-tailed bat)	F. Abrocomidae <i>Abrocoma vaccarum</i> * (Chinchilla rat)
F. Molossidae <i>Sauromys petrophilus</i> * (Flat-headed free- tailed bat)	O. Rodentia	F. Chinchillidae <i>Chinchilla brevicaudata</i> * (Chinchilla) <i>Lagidium viscascia</i> * (Mountain vizcacha)
O. Primates	F. Caviidae <i>Kerodon rupestris</i> * (Rock cavy) <i>Galea spixii</i> (Cavy)	F. Muridae <i>Akodon andinus</i> <i>Eligmodontia typus</i> <i>Graomys griseocephalus</i> <i>Phyllotis darwini</i> *
F. Cercopithecidae <i>Papio ursinus</i> (Chacma baboon) <i>Cercopithecus aethiops</i> (Vervet monkey)	F. Dasyproctidae <i>Dasyprocta prymnolopha</i> (Agouti)	O. Carnivora
O. Hyracoidea	F. Echimyidae <i>Thrichomys apereoides</i> * (Punaré)	F. Canidae <i>Pseudalopex culpaeus</i> (Andean red fox)
F. Procaviidae <i>Procapra capensis</i> * (Rock dassie)	O. Carnivora	F. Mustelidae <i>Galictis vittata</i> (Grison)
O. Rodentia	F. Canidae <i>Cerdocyon thous</i> (Forest fox)	F. Felidae <i>Lynchaillurus pajeros</i> (Pampas cat) <i>Felis concolor</i> (Puma)
F. Petromuridae <i>Petromus typicus</i> (Dassie rat)	F. Mustelidae <i>Galictis vittata</i> (Grison) <i>Conepatus semistriatus</i> (Hog-nosed skunk)	
F. Muridae <i>Aethomys namaquensis</i> * (Namaqua rock mouse) <i>Petromyscus collinus</i> * (Pygmy rock mouse)	F. Felidae <i>Felis concolor</i> (Puma) <i>Felis yagouaroundi</i> (Jaguarundi) <i>Felis onca</i> (Jaguar)	
F. Hystricidae <i>Hystrix africaeaustralis</i> (Porcupine)		
O. Lagomorpha		
F. Leporidae <i>Pronolagus rupestris</i> * (Smith's red rock rabbit)		
O. Artiodactyla		
F. Bovidae <i>Oreotragus oreotragus</i> * (Klipspringer) <i>Oryx gazella</i> (Gemsbok)		
O. Carnivora		
F. Canidae <i>Vulpes chama</i> (Cape fox) <i>Canis mesomelas</i> (Black-backed jackal)		
F. Mustelidae <i>Ictonyx striatus</i> (Striped polecat) <i>Helogale parvula</i> (Dwarf mongoose)		
F. Hyaenidae <i>Crocuta crocuta</i> (Spotted hyaena) <i>Hyaena brunnea</i> (Brown hyaena)		
F. Felidae <i>Felis libyca</i> (African wild cat) <i>Felis nigripes</i> (Small spotted cat) <i>Panthera pardus</i> (Leopard)		

mammals (*i.e.* an effect on the abiotic components of the habitat). The rocks contribute to environmental complexity in a number of ways. They offer sites for shelter, where both small and large mammals may place their nests or dens to raise their young in a stable microclimate that is relatively secure from predators and competitors. For example, in a remarkable example of

convergent evolution, the granite outcrops of Namibia support a small rock-specialized molossid bat, *Sauromys petrophilus*, that has an extremely flat body and is adapted to live in the cracks of exfoliating granite (Skinner & Smithers 1990). In the Caatinga, there is also a flattened molossid bat, *Molossops mattogrossensis*, that is specialized for living in exfoliating granite (Willig &

Table 2

Genera of rock-specialist mammals inhabiting granitic outcrops in Namibia (in the general environs of Gobabeb); in the Brazilian Caatinga (near Exu, Pernambuco); and in the Andes of central Argentina (Mendoza Province). These species, representing among the three areas 6 orders and 11 families, and including 4 endemic families and 9 endemic genera (endemic to the rocky areas in the region) would not be in the arid area in question if the rock resource were not present.

Namibia	Caatinga	Andes
<i>Elephantulus</i> *	<i>Molossops</i> *	<i>Abrocoma</i> *
<i>Sauromys</i> *	<i>Kerodon</i> *	<i>Lagidium</i> *
<i>Pronolagus</i> *	<i>Thrichomys</i> *	<i>Chinchilla</i> *
<i>Procavia</i> *		
<i>Petromus</i> *		
<i>Petromyscus</i> *		
<i>Oreotragus</i> *		

Jones 1985). By virtue of their elevation above the surrounding habitat, rock outcrops also offer sites for observation posts, where predators can be detected, or territorial communication can occur. For example, the hyraxes of Namibia, the caviids of the Brazilian Caatinga, and the chinchillid rodent (*Lagidium*) of the Argentine Andes (Pearson 1948) are all diurnal herbivores that use the rocks for observation points to detect predatory attacks from the air or from the ground. All use sentinels that give warning calls as predators are sighted (Mares & Lacher 1987). Similar behavior in using the structure of the rocky habitat has been shown for the petromurid rodent, *Petromus*, in Namibia, and many other species as well (Mares & Lacher 1987). Even large mammals, such as the spotted hyaena (Family Hyaenidae, *Crocuta crocuta*) and the klipspringer (Family Bovidae, *Oreotragus oreotragus*) use the rocks for dens (hyaena) or for lookout posts (antelope). Additionally, the rocks offer sites for chemical communication, where communal defaecation piles, a common trait of rock-dwelling mammals (Mares & Lacher 1987), may function in territorial and other communication by elevating the piles of faeces high in the air where the scent can be carried for long distances; see, for example, Branch (1993) for information on how the plains vizcacha (Chinchillidae, *Lagostomus maximus*), a relative of the mountain vizcacha, *Lagidium*, uses communal sites for pheromonal communication. The rocky substrate also functions as sites for capturing water. Granitic outcrops may capture and hold rainfall for extended periods, and this water is important to mammals in arid regions. Additionally, the rocks may act to permit condensation of fog in some areas (e.g. Namibia), thus increasing water availability to mammals (Withers 1979). Rocks also provide sites that are defensible by males, or by groups of related individuals. Mares & Lacher (1987) showed that rock-piles, and the shelter and other resources they offer, are defensible by males of several species, thus permitting them to accrue harems of females by apportioning the rock resource differentially on the basis of sex. How extensive harem formation may be in rock mammals is not yet clear, but it is clearly not uncommon among species inhabiting rocky areas, although it does not appear to be a common reproductive pattern among small mammals that do not defend rocks.

Microclimate. Rocky areas that occur within a more-xeric region offer mesic refugia through microclimate effects. These can also be considered first-level effects of the rocks on the mammal community. Water accumulated by rocks would contribute to micro-changes in humidity. The shelter offered by the rocks, especially in areas where run-off water or fog condensation may accumulate (Withers 1983), will also tend to increase humidity, and thus reduce water loss for mammals that utilize the shelters during arid periods. Similarly, the rocks offer shade during the heat of the day, and a cool refuge during summer or during the dry season. Alternatively, the rocks store heat, thus modifying the microclimate of shelters during cold periods by keeping temperatures elevated above that of the cold desert air. The rocks provide elevated areas where temperature increases rapidly in the morning sun, thus providing points of rapid warming, where mammals can increase their body temperatures quickly before beginning the day's activities. Most rock mammals have been observed to bask in the early morning (Mares & Lacher 1987). Rocks, particularly those that offer deep shelters, provide temperature stability from the outside air which, in arid areas, can undergo pronounced fluctuations. For example, Mares (1975) reported air temperature changes of up to 38 °C over a 24-hr period in the Andes of northwestern Argentina. Rock-piles also provide a diel factor to microclimate, permitting animals to choose from a selection of microclimates throughout the day and night. Because of the structure of rock-piles, animals can utilize different portions of the rocks at different times of day to increase the climatic variability (or stability) of their habitat. For example, sunny portions of the rocks can be used for warming up for some animals, while at the same time others are cooling down in shaded portions. During very wet weather, dry portions of the rock habitat can be sought by mammals when other microsites are too wet for the species in question.

Effects of rock-piles on vegetation. Perhaps one of the most evident second-level effects of rock-piles on mammal communities in an arid region is the effect of the rocks on vegetation. In an area such as the Caatinga, for example, rock-piles support small forests of trees that largely remain green throughout the extended droughts. During wet periods, these refugial forests may be less noticeable, imbedded as they are within the brilliant green scrub forest of the Caatinga, but during droughts, almost the only green vegetation remaining over vast areas is that associated with the rock-piles (Mares *et al.* 1985a). Similarly, in Namibia, the rocks have been shown to support more complex vegetation than much of the surrounding desert (Seely 1987, 1990; Withers 1979). The vegetation of the rocks is often greener for longer periods due to increased water availability afforded by the rocks. Additionally, the granitic outcrops support perennial trees in zones where most of the other vegetation may be low scattered shrubs or short-lived ephemeral plants. The vegetation permits the browsing habit to develop among small mammals (and larger mammals, as well). Thus such disparate species as hyraxes (Order Hyracoidea), rabbits (Order Lagomorpha), and rodents (Order Rodentia) all have evolved rock specialists that browse on the trees and shrubs associated with the rock-piles. Of course, the vegetation contributes enormously

to both habitat complexity, habitat stability, and microclimate. In the Caatinga, the rock-piles are assumed to offer refugia for rock specialists and a wide variety of species that are not rock specialists during periods of drought (Mares *et al.* 1985a). Plants associated with rocks thus offer food, shelter, and other major components of mammal niches throughout the year.

Effect of rocks on mammal species richness

As noted, the rocks have significant effects, both first- and second-level, on mammal communities and on major components of mammal niches, including food, shelter, and microclimate. The rocks, their plants, and their special microclimate, make it possible for many species either to specialize on the rocks and their associated resources (Mares & Lacher 1987), or to live in the rocks when the surrounding habitat is marginal due to drought or other factors (*e.g.* Withers 1979; Streilein 1982a; Mares *et al.* 1985a). The rocks and their vegetation make possible, for example, a richer invertebrate community, including many insects and arthropods, thus making this group of organisms available to mammalian predators. Thus the existence of certain communities of mammals are only possible because of the rock component of the habitat (Table 2), a fact that can be considered a third-level effect of the rocks on species richness. This community may consist of diurnal browsing rock specialists, such as hyraxes and petromurids in Namibia, caviids and echimyids (*Thrichomys*) in the Caatinga, or chinchillids and abrocomids (*Abrocoma*) in Argentina. However, the rock habitat influences much more than just rock specialists. In Namibia, among small mammals, the rocks harbor *Aethomys*, an insectivorous murid rodent, and *Elephantulus* (Order Macrosceloidea), an insectivorous elephant shrew (Withers 1979). In the Caatinga, the rocks support an invertebrate-feeding marsupial, *Monodelphis domestica* (Streilein 1982a), and in the Andean mountains at lower elevations (up to 2 000 m) insectivorous mouse opossums (genus *Marmosa*) also inhabit the rocks (Mares *et al.* 1989). Thus the rocks add to the complexity of the small mammal community, as well as to the vegetative, structural, and climatological complexity of the habitat itself. Larger mammals, such as the klipspringer (noted above, in Namibia; Tilson 1980), the huemul deer (*Hippocamelus*) in the Andes (Merkt 1987; Barquez *et al.* 1991), and a deer (*Mazama gouazoubira*) in the Caatinga frequent the rocky habitats, especially during dry weather (Mares *et al.* 1985; T E Lacher Jr, *pers. comm.*).

As the bats, herbivores, microomnivores, and insectivores inhabit the rocks, the habitat becomes increasingly attractive to carnivores, who can forage on the inhabitants of the rocks and adjacent areas. This can be considered a fourth-level effect of the rocks on mammalian species richness. (Of course, carnivores also respond to the rocks for shelter, microclimate, and water, as do other mammals.) In Namibia, for example, the rocks harbor many carnivores, including the leopard *Panthera pardus*, the spotted hyaena, the African wild cat *Felis lybicus*, the black-backed jackal *Canis mesomelas*, and others (Coetzee 1969). In the Caatinga of Brazil, a canid, two mustelids, and several cats frequent the rocky habitat in order to prey on the species of vertebrates and invertebrates that are associated with the rocks. In Argentina, the same families, canids, mustelids, and cats,

frequent the rocky outcrops, many obtaining some of their principal foods from species living in the rocks.

Discussion

The influences of granitic outcrops on patterns of local and regional mammal diversity and ecology are pervasive. In comparing this very similar habitat in quite different environments, it becomes clear that rocks make it possible for a wide variety of rupicolous species to evolve. These species bring with them a high degree of specialized adaptations (and genetic information) to the rupicolous habit that is not present in species in the surrounding habitat. In fact, the rocks provide an important niche component that can only be readily exploited by rock specialists which have developed the special abilities required to live largely or only in rocks (Mares & Lacher 1987). This means that these species, from numerous orders and many families, evolutionarily opt to exploit the rock resource and the microenvironment associated with it. By selecting this evolutionary path, the species are able to persist in regions that would otherwise be more challenging (and support fewer species) due to the generally arid environment (Namibia, the high Andes), or because of the periodic devastating droughts (the Caatinga). Those species that are able to specialize on the rock resource in these regions also appear to move into longer-term ecological strategies, where life spans exceed one year (unlike most boom-and-bust) small mammals, and where microclimatic stability leads to complex morphological, ecological, and behavioral traits to persist in the specialized rock habitat. Once this community of mammals has developed, it becomes possible for species associated with them (*e.g.* carnivores) also to become regular components of the rock-associated mammal community.

Thus at a local level, granitic outcrops lead to an increase not only in the numbers of species supported in an area, but in higher-order diversity as well. More families and even orders of mammals are able to occur in an area because of the presence of the rocks. Additionally, those species that have evolved to live in rocks are often so specialized that they are endemic to the rocks; no rocks, no species and, in many cases, no genera, families or orders either. This has significant implications for research in conservation biology. Although much attention has been paid to the presence or absence of species as an important measure of a habitat's importance, habitats that contain endemic species (or families or orders) are much more important to maintain than habitats that merely support many species (Mares 1992). Mares made this argument for a comparison between drylands and tropical forests in the Neotropics, but the same argument can be extended to the unique fauna of rocky outcrops as well.

Because rocks open up a series of major new niches in an area, and because to specialize on the rock resource demands a host of unusual adaptations, those species that have taken this evolutionary step become quite different genetically from their nearest relatives. So different, in fact, that their nearest relatives are often in other genera or even families. This is the higher order diversity that was discussed by Mares (1992). When comparing a

tropical and two temperate regions on two different continents, the faunistic evolutionary pattern that appears is similar. Rocks lead to specializations among mammals, which leads to large series of unique adaptations, often quite distinct from their nearest relatives. The rocks also lead to the formation of communities of these specialized mammals that differ greatly in their suites of adaptations from species in the surrounding non-rock habitat. Because the rocks are an ancient habitat and have likely impelled this evolutionary process to begin long ago, rock specialists are phylogenetically unique as well, and the degree of endemism is high at the species level, and at higher taxonomic levels. This results in faunas that contain a great deal of unique genetic material in areas that are quite limited geographically. These should be areas of intense conservation interest. These influences are apparent at both the local and regional level. Indeed, it would be interesting to compare the contribution of rock-dwelling mammals to global diversity not only at the species level, but at levels above the species. Initial indications are that the contribution of rock-piles to global mammal diversity would be quite high indeed.

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